Rhodora

JOURNAL OF THE

NEW ENGLAND BOTANICAL CLUB

Vol. 63 March, 1961 No. 747

AN ECOLOGICAL INTERPRETATION OF RHODODENDRON COLONIES IN MAINE AND NEW HAMPSHIRE

A. R. Hodgdon and Radcliffe Pike

Over a large part of its natural range *Rhododendron maximum* is a local or rare species occupying certain unique habitats. Thus its disjunct distribution in the peripheral part of its range can be explained in part by the discontinuity of possible habitats. But after making extended observations of rhododendrons in central and northern New England we have seen that there are many more apparently suitable places for the species to grow than there are colonies. One explanation of this interesting fact might be that wind dispersal results in the establishment of new colonies only here and there as the minute seeds are fortuitously blown into new areas. Yet wind dispersal for great distances does not seem to warrant much consideration due first to the very protected and nearly windless sites in which the Maine and New Hampshire colonies are found and our failure to find seedling reproduction beyond one to two hundred feet away from mature plants. We might more reasonably account for the more disjunct colonies on the basis of their being relics of an earlier more continuous distribution of the species, the assumption here being that various disturbances have occurred to destroy them in many of the swampy areas that now seem to be entirely suitable for them. The recent fluctuations in size of a number of rhododendron col-

Published with the approval of the Director of the New Hampshire Agricultural Experiment Station as Scientific Contribution No. 263.

onies in Maine and New Hampshire as reported by us recently[1] give some support to the contention that a great decline in both number and size of colonies could indeed have resulted from the climatic changes that are known to have occurred many times in the post glacial period. A recent review[2] points up the nature of some of these climatic oscillations. The data presented in this paper make it seem likely that the limits of tolerance of rhododendron for certain climatic factors have been exceeded locally during some of the more severe climatic minima. At two periods in post glacial times climatic conditions were apparently such as to make possible the northward migration of warmer floras. These moderate periods were followed by decidedly colder more rigorous climatic conditions. For rhododendron to have persisted as a relic, one must postulate not only a once wider and more general distribution which could conceivably have occurred during these two warmer periods but also a continuity of suitable habitats from the time when the species was more or less continuously distributed.

There have been several papers on *Rhododendron maximum* emphasizing its distributional peculiarities and something of its ecology. Recently Iltis[3] has discussed interestingly and in some detail an outlying colony in the Coastal Plain of Virginia below Fredericksburg. He found that the majority of common species of associated trees and shrubs there were also among the dominant species listed by Spencer[4] in his study of 36 New Jersey Colonies and by Griggs[5] for the Sugar Grove Region of Ohio. The Virginian

---

[1]Hodgdon, A. R. and Pike, R. "Recent Changes in Some Rhododendron Colonies in Maine and New Hampshire". Rhodora **62**: 87-93, April 1960.

[2]Dorf, Erlig. Climatic Changes of the Past and Present. American Scientist 48: 341-364, September 1960.

[3]Iltis, Hugh H. Studies in Virginia Plants II. *Rhododendron maximum* in the Virginia Coastal Plain and its Distribution in North America. Castanea **21**: 114-24, September 1956.

[4]Spencer, Ernest L. "Natural distribution of *Rhododendron maximum* in New Jersey". Bull. Torr. Bot. Club **59**: 401-24, 1932.

[5]Griggs, R. F. A Botanical survey of the Sugar Grove Region. Ohio State University Bull. **18** (25) : 273-75, 328, 1914.

TABLE I. Colonies of *Rhododendron maximum* in Maine and New Hampshire. (The first 7 stations listed are in Maine, the others are in New Hampshire).

Location "Township"	Characteristics of site	Size (estimated)
1. Lexington	Swamp and south facing slope mostly swamp (seedlings)	½ acre
2. Standish (1)	Swamp and south facing slope mostly swamp (seedlings)	3½ acres
3. Standish (2)	Swampy woods (seedlings)	½ acre
4. Standish (3)	Well drained ridge adjacent to swamp	1/12 acre
5. Standish (4)	Swampy woods	1/20 acre
6. Acton	Gently south facing and well drained slope	10 x 6 ft.
7. Sanford	North facing slope of about 20% in steepest part (seedlings)	5 acres
8. Albany	Steep north facing mossy and wet ledges (seedlings)	1/3 acre (concentrated); few plants scattered over acre.
9. Pittsfield-Barnstead	Swampy wooded pond north-facing shore (seedlings)	1/3 acre
10. Grantham	Swampy woods (seedlings)	¾ acre
11. Manchester (1)	Slope at eastern edge of swamp and in swamp: reported to have covered formerly scores of acres in swamp (seedlings)	2 acres on slope, acreage in swamp uncertain but plants decidedly scattered there.
12. Manchester (2)	Slope facing northeast	¼ acre
13. Manchester (3)	Swampy woods and bed of stream	½ acre
14. Hopkinton	Moist but scarcely swampy woods	1/16 acre
15. Mason	Swamp and adjacent west facing slope mostly swamp (seedlings)	7 acres
16. Wilton	Northerly slope and bank of stream (seedlings?)	1/3 acre
17. Fitzwilliam	Mostly swampy woods but also adjoining slopes and ridges (seedlings)	15 acres
18. Richmond	Swampy woods said to have covered 7-8 acres formerly (seedlings)	1½ acres
19. Harrisville	Swampy woods (seedlings)	½ acre

Colony resembled the New Jersey stands also in having a strongly acid soil, pronounced shade and abundant water. Iltis agreed with Spencer's conclusion for New Jersey that the distribution of *R. maximum* in Virginia is governed by topography and not by climate. It should further be noted that the Virginia colony, all of those in New Jersey reported by Spencer and those in Ohio mentioned by Griggs (see references) are on north-facing slopes or, in the case of a few in New Jersey, in swamps.

During recent field work we have recorded for each of our 19 Maine and New Hampshire colonies, such facts as the associated woody species, the absence or presence of seedling rhododendrons, the nature of the habitat — whether swamp or slope and, if so, the direction of slope as well as some other features. We are now in a position therefore to evaluate the ecological requirements of *R. maximum* by comparing our colonies with those discussed by Iltis, Spencer and Griggs. Since we had no reason to doubt that the soils in all colonies were definitely acid and moreover because of the mass of scientific evidence that shows the oxylophytic character of the species, we decided at the outset not to include pH determinations as part of the record. We did attempt to determine the area of each stand, however, to provide a basis for evaluating the changes that may occur in the future.

TABLE I.

Table I shows 11 of our colonies to be chiefly in swamps, one other (Manchester (1)) divided between a swamp and an adjoining east-facing slope, 4 colonies on north-facing slopes, 2 very small colonies in non-swampy woodland and 1 small stand on a south-facing slope. But it should be remarked that of the 11 swamp-colonies, 2 have excellent rhododendrons on their adjacent south-facing slopes and another has prolific plants on the west-facing adjacent slope. In contrast to the situation in New Jersey, the Coastal Plain of Virginia and in Ohio, swamps generally provide better habitats for rhododendrons in Maine and New Hampshire than do slopes. Also with us the direction of slope does not seem to be critical. We have pointed out elsewhere[6] that juxtaposition of swamps and adjacent slopes as alternative habitats for rhododendrons in many of the finest Maine and New Hampshire colonies may provide the species with a means of surviving environmental changes.

Seedlings were noted in all of the larger colonies in Maine and New Hampshire and in some of the smaller stands as

---

[6]Hodgdon, A. R. and Pike, R. "Recent Changes in Some Rhododendron Colonies in Maine and New Hampshire". Rhodora **62**: 87-93, April 1960.

well. Thirteen colonies (more than 68%) had seedlings in contrast to the situation in New Jersey where Spencer reported seedlings in only 5 of his 36 stations (less than 14%). Since Spencer's observations were made about 30 years ago we are led to speculate on the present condition of the New Jersey stands as a result of the tendency for temperatures in Northeastern United States to rise appreciably between

TABLE II. List of tree-species associated with *R. maximum* in Maine and New Hampshire Stations: X indicates presence*

	Lexington	Standish (1)	Standish (2)	Standish (3)	Standish (4)	Acton	Sanford	Albany	Pittsfield-Barnstead	Grantham	Manchester (1)	Manchester (2)	Manchester (3)	Hopkinton	Mason	Wilton	Fitzwilliam	Richmond	Harrisville
Acer rubrum	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Tsuga canadensis	X	X	X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X
Betula lutea	X	X	X		X		X	X		X	X	X	X	X	X		X	X	X
Betula papyrifera		X	X	X			X	X	X		X		X		X	X	X		X
Fagus grandifolia		X	X	X		X	X	X	X		X			X	X			X	
Pinus strobus			X	X		X					X	X	X	X	X	X	X	X	X
Quercus rubra		X		X		X	X		X		X	X		X		X			X
Picea rubens			X	X	X			X		X	X						X	X	X
Nyssa sylvatica		X	X	X			X				X				X		X		X
Betula lenta									X		X		X		X		X		
Fraxinus nigra	X	X								X							X		X
Fraxinus americana			X	X									X		X				
Abies balsamea		X			X					X							X		
Quercus alba						X						X	X						
Acer saccharum									X							X			
Castanea dentata										X		X							
Betula populifolia								X					X						
Populus grandidentata							X										X		
Pinus resinosa										X									
Thuja occidentalis	X											X							
Chamaecyparis thyoides			X																
Quercus velutina													X						
Q. coccinea															X				
Q. prinus														X					
Carpinus caroliniana						X													
Ostrya virginiana														X					
Ulmus americana																	X		
Populus tremuloides																	X		
Prunus pennsylvanica																	X		
Prunus serotina																			
Tilia glabra																			X

* The nomenclature in this paper follows that of Gray's Manual of Botany, 8th edition, 1950.

the years 1930 and 1955.[7] Such temperature rise might easily further reduce areas suitable for seedling reproduction as our observations indicate that *R. maximum* seedling reproduction takes place only on mossy generally moist sites.

Tables IV and V, which compare the associated species of woody plants growing along with *Rhododendron maximum* in the 4 areas under consideration, point up certain similarities, notably the almost universal presence of *Acer rubrum* and the rather high frequency of *Tsuga canadensis*. *Kalmia latifolia*, *Cornus florida* and *Quercus alba* are the three other species that are present in more than half of the New Jersey

TABLE III. List of shrub-species associated with *R. maximum* in Maine and New Hampshire Stations.

	Lexington	Standish (1)	Standish (2)	Standish (3)	Standish (4)	Acton	Sanford	Albany	Pittsfield-Barnstead	Grantham	Manchester (1)	Manchester (2)	Manchester (3)	Hopkinton	Mason	Wilton	Fitzwilliam	Richmond	Harrisville
Hamamelis virginiana	x	x	x						x		x	x		x	x			x	
Viburnum cassinoides			x	x	x		x		x				x				x	x	x
Viburnum alnifolium	x		x		x		x		x		x								
Nemopanthus mucronata		x			x		x										x	x	x
Acer pensylvanicum		x	x		x			x			x								
Vaccinium corymbosum							x		x		x			x				x	
Ilex verticillata							x			x	x	x							x
Kalmia latifolia											x				x		x	x	
Acer spicatum		x						x		x									
Kalmia angustifolia							x		x					x					
Epigaea repens var. glabrifolia			x								x			x					
Linnaea borealis var. americana			x						x								x		
Alnus rugosa										x		x							
Lyonia ligustrina											x							x	
Vaccinium angustifolium											x			x					
Salix Bebbiana										x									
Lindera Benzoin													x						
Sassafras albidum											x								
Pyrus floribunda																			x
Amelanchier laevis							x												
Rhus radicans													x						
Vaccinium myrtilloides									x										
Lonicera canadensis				x															
Viburnum recognitum												x							
Sambucus pubens								x											

[7]Braun, E. L. Deciduous Forests of Eastern North America, Blakiston, 1950.

stands and might therefore be regarded as being characteristic associates of rhododendron in that area. However *C. florida* is absent from all Maine and New Hampshire colonies, occupying instead only certain well drained and warm exposures often with *Quercus velutina* — very different sites indeed from those of rhododendron. Mountain Laurel is similarly a disjunct species over most of its Maine and New Hampshire range; again it is adapted there to better drained

TABLE IV. Presence of Common New Jersey woody species in four Rhododendron areas: the figure given is the percent of stands (to the nearest full number) in which a species was observed; × = present

Species	New Jersey Spencer 1932	Maine and New Hampshire	Ohio Griggs 1914	Virginia Iltis 1956
Acer rubrum	94	100	×	×
Tsuga canadensis	72	95	×	—
Kalmia latifolia	69	21	×	×
Cornus florida	61	—	×	×
Quercus alba	58	16	×	×
Quercus velutina	42	5	×	—
Q. Prinus	42	5	×	—
Betula lenta	39	26	×	—
B. lutea	39	79	—	—
Fagus grandifolia	28	58	×	×
Liriodendron tulipifera	25	—	×	×
Chamaecyparis thyoides	5.5	5	—	—

habitats though occupying the same general range. *Quercus alba* on the other hand is a common forest tree in much of southern New Hampshire and southwestern Maine; yet it is met with in only 3 of the nineteen colonies; it too grows more commonly in drier places.

Of the remaining so-called "Common Species" *Betula lutea* is associated with rhododendron in 15 of our 19 stands though it is present in only 14 of the 36 New Jersey colonies and it is not mentioned by Griggs in Ohio nor is it present in the Virginian Colony studied by Iltis. *Fagus grandifolia* seems to do a bit better being present in all 4 areas but occupying only 10 stands out of 36 in New Jersey and 11 of our 19. Of the other prevalent species in the Ohio, New Jersey and Virginia stands, *Liriodendron tulipifera* does not

extend north of southern New England while *Quercus Prinus* barely gets into southern New Hampshire and Maine.

Turning to the commonest Maine and New Hampshire associates, aside from those already mentioned, we find several species that would be found very rarely if at all in the

TABLE V. Presence of Common New Hampshire Woody species in four Rhododendron areas

Species	Maine and New Hampshire	New Jersey	Ohio	Virginia
Acer rubrum	100	94	×	×
Tsuga canadensis	95	72	×	—
Betula lutea	79	39	—	—
Betula papyrifera	63	—	—	—
Fagus grandifolia	58	28	×	×
Pinus strobus	63	—	—	—
Quercus rubra	53	—	—	×
Hamamelis virginiana	47	sometimes present	×	×
Picea rubens	47	—	—	—
Viburnum cassinoides	47	—	—	—
Nyssa sylvatica	42	—	×	—
Viburnum alnifolium	32	—	—	—
Betula lenta	26	39	×	—
Fraxinus nigra	32	—	—	—
Nemopanthus mucronata	32	—	—	—
Acer pensylvanicum	26	—	—	—
Vaccinium corymbosum	26	—	—	—

other 3 areas. Such include *Betula papyrifera*, *Pinus strobus*, *Viburnum alnifolium*, *Picea rubens* and *Viburnum cassinoides*.

In Braun's "Deciduous Forests of Eastern America" frequent mention is made of the types of forest communities in which *Rhododendron maximum* occurs, *Tsuga canadensis* being usually a dominant tree where rhododendron is found and *Acer rubrum* occurring commonly. The presence of other species of trees depends on the peculiarities of the habitat and the geographical area in which the rhododendrons are found. These also are the only two species that appear repeatedly in a majority of colonies under consideration in this paper. Of the 15 other commonest associated species of trees in Maine and New Hampshire 11 are absent

in New Jersey, 11 in Ohio and 13 in the Virginian Coastal Plain, the remaining species having no high order of coincidence in these places either.

For local parts of the range of *Rhododendron maximum* there seems to be some usefulness in recognizing a characteristic rhododendron association, because the same group of associated species of plants is met with over and over again. But over the whole range the associates may change markedly; the nearly ubiquitous Tsuga may give way to *Picea rubens* at one extreme of climatic tolerance of rhododendron or to *Chamaecyparis thyoides* at another.

Good[8] has stated that each species has its particular range of tolerance. As a corollary it may be assumed that no two species, unless they are mutually dependent, have precisely the same range of tolerance of environmental conditions. A consideration of the associated woody species growing with *Rhododendron maximum* in various parts of its range lends support to this contention. Obviously none of the associated species has precisely the same tolerance of environmental factors as *R. maximum*. Those that are most frequently associated with it over its entire range are those that presumably most closely approach it in tolerance. But many of the common associated species in any one part of the range have very different amplitudes of environmental tolerance from that of rhododendron and therefore will be absent from climatically different parts of the range. It seems preferable to interpret the facts of the *Rhododendron maximum* "association" in this way rather than to try to contrive a definite rhododendron association to embrace any considerable portion of the area that it occupies. On the other hand, it is to be expected that whenever environmental conditions are somewhat similar there will be essentially the same associates unless indeed these associates have had a different history and followed different migrational paths. It can be seen then that *Tsuga canadensis* and *Acer rubrum* have ranges of tolerance somewhat similar to that of *R. maximum*. But *Betula lutea* and other northern associated

[8]Good, R. A Theory of Plant Geography. New Phytologist 30: 155, 1931.

species have ranges of tolerance overlapping that of *R. maximum* only in the northern States.

We must conclude from this comparison of *Rhododendron maximum* colonies in 4 outlying parts of its range that 1. There is no single physiographic situation to which the species is confined so long as an abundance of moisture is available. 2. There is no such thing as a predictable association of species with which *Rhododendron maximum* is constantly to be found. 3. Within any particular climatic zone the rhododendron association is usually composed of essentially the same dominant species and often occupies similar physiographic situations. 4. The suggestion is made that Good's concept of tolerance suggests a reasonable explanation of the observed diverse character of the rhododendron association.

— DEPARTMENT OF BOTANY AND DEPARTMENT OF HORTICULTURE, UNIVERSITY OF NEW HAMPSHIRE, DURHAM, NEW HAMPSHIRE.

TAXONOMIC FERN NOTES. I

ROLLA TRYON

1. **Adiantum humile** Kze.

The name *Adiantum humile* Kze., based on a Poeppig collection from Peru, has seldom appeared in the literature since it was first published and to my knowledge has never been treated in a definitive manner. Mettenius identified *Lechler 2319* and *2319a* (B!) from Peru as *A. humile* but he did not publish these identifications in *Filices Lechlerianae;* the specimens are *Adiantum terminatum* or a variant of it.

An authentic specimen of *Adiantum humile* is at Vienna and a photograph of this specimen and fragments from it were obtained for the British Museum (Natural History) by the late A. H. G. Alston. This specimen has a valid claim to represent the name since the holotype was presumably destroyed with the Herbarium at Leipzig and since it is perhaps the only authentic material now extant (I saw no type material at B, BM, K, L, LE, P, S-PA, or U). I studied this authentic material and it unquestionably represents the spe-